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Interacting effects of grass height and herbivores on the establishment of an encroaching savanna shrub

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Abstract Shrub encroachment is a widely observed problem in Southern African savannas. Although the effects of herbivory and grass height on woody species recruitment have been studied individually, little information exists about how these factors interact. In this study seeds and seedlings of the encroaching shrub *Dichrostachys cinerea* were planted in clipped and unclipped grass plots, with and without large herbivores present. Seed germination, seedling survival and seedling predation were monitored for 8 months. Germination started earlier in plots where herbivores were excluded. Overall, the earlier the seeds germinated, the longer the seedlings survived. Clipping positively affected the number of germinated seeds, seedling growth and survival but effects varied among herbivore exclusion treatments and sites. Invertebrates caused the majority of the seedling damage. We conclude the recruitment of *D. cinerea* is influenced by the interplay of grass height and herbivory. In this study, the presence of large herbivores early in the wet season, and the absence of simulated grazing later on, affected the regeneration of *D. cinerea* negatively. However, differences in effects among sites suggest that the mechanisms found here may work differently in other habitats.

Keywords Bush encroachment · *Dichrostachys cinerea* · Herbivory · Precipitation · Seed germination · Seedling survival

Nomenclature *Dichrostachys cinerea* (L.) Wight and Arn. · *Digitaria longiflora* (Retz.) Pers. · *Eragrostis curvula* (Schrad.) Nees · *Eragrostis superba* Peyr. · *Panicum maximum* Jacq. · *Sporobolus africanus* (Poir.) A. Robyns and Tournay · *Sporobolus nitens* Stent · *Themeda triandra* Forsk. · *Urochloa mosambicensis* (Hack.) Dandy

Introduction

Bush and tree encroachment poses significant problems to farmers and wildlife managers in many parts

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of the world and has been well documented in North America (Hobbs and Mooney 1986; Archer et al. 1988; Archer 1995), South America (Adamoli et al. 1990), Australia (Burrows et al. 1990) and Africa (Van Vegten 1983; Watson and MacDonald 1983; Skarpe 1990; Prins and van der Jeugd 1993; Moleele et al. 2002). Particularly in formerly open grasslands an increase in woody plant biomass can alter the water balance (Pressland 1973), fire intensity (van Langevelde et al. 2003), nutrient cycling (Belsky 1992), and primary productivity of the grass layer (Stuart-Hill and Tainton 1989). As livestock and large herbivores are highly dependent on the quality and quantity of grass (Coe 1983; Demment and van Soest 1985; Belovsky 1997), they are also likely to be negatively affected by bush encroachment. In South Africa it has been estimated that 13 million ha of savanna have been subject to recent bush encroachment (Trollope et al. 1989) due to changed grazing and fire regimes.

Herbivores and fire are the two major interacting drivers of tree–grass dynamics in African savannas (Pellew 1983; Dublin 1991; McNaughton 1992). Grazers can indirectly and positively affect tree seedling establishment by reducing the surrounding grass cover (Roques et al. 2001; Goheen et al. 2004). This decreases competition with grasses for resources such as water, nutrients and light (Belsky and Blumenthal 1997) and prevents seedlings from burning through reduced fuel loads (Walker et al. 1981; van Vegten 1983; Archer 1995; Milton and Dean 1995). Fire may additionally promote the regeneration of woody plant species by promoting the release and germination (Brown and van Staden 1997; Keeley and Fortheringham 2000; Brown et al. 2003) of seeds. Consumption of seed pods followed by defecation of intact seeds by browsers can also promote shrub recruitment (Brown and Archer 1987; Reyes et al. 1994) as scarification through ingestion is known to break seed dormancy (van Staden et al. 1994b). On the other hand, large herbivores can inhibit tree establishment directly through browsing, uprooting or trampling of seedlings (Dublin et al. 1990; Mwalyosi 1990; Sinclair 1995). High browsing pressure by selective herbivores (such as impala) can prevent the establishment and recruitment of woody seedlings (Prins and van der Jeugd 1993) and make them more exposed to fire (Mills 1983). Furthermore intense grazing can lead to a drier microclimate and lower soil moisture which increases the risk of seedling desiccation, especially in the dry season. In addition to large herbivores, smaller consumers (e.g. rodents and insects) have been reported to negatively influence recruitment of woody species via seed- and seedling predation (Sullivan 1979; Andersen and Lonsdale 1990; Ostfeld and Canham 1993; Miller 1994; Auld 1995; Crawley and Long 1995; Harju and Tahvanainen 1997; Weltzin et al. 1997; Manson et al. 2001), especially during population peaks (Pusenius et al. 2000). Although the effects of herbivory and grass height on the recruitment of woody species in savannas have been studied individually (Walker et al. 1981; Trollope 1984; Prins and van der Jeugd 1993; O'Connor 1995), the importance of interactions among these factors is still poorly understood, and experimental studies are rare.

The leguminous shrub *Dichrostachys cinerea* is an important bush encroacher in South African savannas (van Vegten 1983; O'Connor 1995; Roques et al. 2001; Moleele et al. 2002). In the present study we investigate the direct and indirect effects of mammalian herbivores on *D. cinerea* seed germination and seedling survival in a South African savanna. In field experiments, we manipulated grazing intensity by excluding large herbivores and grass height by clipping at four study sites (two in mesic and two in arid savanna). We assumed the time of year during which germination takes place can be crucial for the survival of the seedling. Seeds that germinate early in the wet season may have better chances to survive, which consequently leads to a higher risk for severe bush encroachment. We hypothesised the survival of established seedlings may then be affected by the height of the surrounding vegetation. In tall vegetation seedlings should be protected from browsing herbivores but in short vegetation they would experience less competition with grasses for water, nutrients and light. On the other hand, in short vegetation grazing herbivores may graze them along with grasses and also make them more visible for browsers. We expected that the presence of large herbivores would decrease seedling establishment through predation particularly in clipped grass where seedlings are more visible. Previous studies have shown that the exclusion of large herbivores leads to increased small mammal densities (Hagenah et al. submitted) which in turn may have a negative impact on tree seedling survival. Therefore, both the effects of grazing intensity and grass height on time of germination and survival time, as well as the

proportions of germinated seeds and surviving seedlings at the end of the wet and dry season, were investigated.

Materials and methods

Study site

This study was conducted between March and December 2004 at the Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, South Africa (28°13′ S/32°00′ E). HiP is a 90,000 ha protected fenced area and consists of the Hluhluwe Game Reserve in the North and the iMfolozi Game Reserve in the South. The altitude in the park ranges from 60 to 750 m (Conway et al. 2001). The climate is coastal and seasonal, with temperatures from ±13°C to ±35°C. Precipitation varies greatly across the year and generally falls between October and March. The mean annual rainfall (measured from 1980–2004) for Hluhluwe is 985 mm (min: 68 mm, max: 4060 mm), whereas in iMfolozi it is 650 mm (min: 2 mm, max: 3200 mm), measured at five weather stations each in Hluhluwe (Gontshi, Gunjaneni, Memorial Gate, Nqumeni and Research Centre) and iMfolozi (Makhamisa, Masinda, Mbuzane, Mpila and Tobothi). The park is characterised by savanna vegetation ranging from open grasslands to closed *Acacia* and broad-leaved woodlands (Brooks and MacDonald 1983). Skowno et al. (1999) documented that the woody plant biomass in HiP has rapidly increased over the last 40 years. *Dichrostachys cinerea* (legume of the Mimosoidae), a deciduous multi-stemmed shrub/small tree (Pooley 1993) is an important bush encroacher in HiP, invading large areas of previously open grasslands (Skowno et al. 1999). The shrub produces highly nutritious leaves and pods and the infructescences have a strong rich aroma that attracts browsers (van Staden et al. 1994a). The seeds of *D. cinerea* are impermeable to water and dormant at release (van Staden et al. 1994b; Witkowski and Garner 2000). Dormancy is mainly broken through diurnal temperature fluctuations, by scarification through ingestion and by bruchid exit holes (van Staden et al. 1994b). A fire management regime is simulating natural fires in the park, in which different areas are burnt with varying frequencies. HiP harbours a high diversity and biomass of indigenous large herbivores including elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis* L.), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), wildebeest (*Connocheates taurinus*), zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus),* kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angansi*), impala (*Aepyceros melumpus*) and warthog (*Phacochoerus aethiopicus*).

Experimental design

The present study utilised herbivore exclosures established at four study sites in HiP within the context of a different study (Bond and Olff, unpublished). Fences 2.50 m tall excluded all mammalian herbivores larger than hares from 40 × 40 m plots of vegetation since early 2000. To quantify small mammal densities, permanent trapping grids inside and outside the exclosure treatment were established ($n = 8$). Overall, the absence of large herbivores leads to a significant increase in small mammal numbers (Hagenah et al. submitted). Furthermore the exclusion of large herbivores resulted in increased grass height at all sites. The grass species that were most frequently dominant in the mesic savanna of Hluhluwe included *Sporobolus africanus* and *Digitaria longiflora*. Other frequently dominant grasses were *Panicum maximum* and *Themeda triandra* (Hagenah et al. submitted). For the arid savanna of iMfolozi the dominant grass species were *Urochloa mosambicensis* and *P. maximum*, but also *T. triandra* and *Sporobolus nitens* were found frequently (all mentioned grass species are C4 species). The amount of rainfall was measured at weather stations situated at our study sites and varied seasonally (Fig. 1). In 2004 the amount of rainfall was similar to that of previous years since 1980, described in the *study site* section. The soils at all study sites were lithosols with ca. 17% clay content (FAO). All study sites are burned every second year; in 2004 they were burnt approximately 4 months after seeds and seedlings were planted. *D. cinerea* can survive bushfires and resprouts easily after burning (Bond, pers. comm.).

Seed-germination and seedling survival experiments

Fresh seeds of *D. cinerea* were collected during July to September 2003 from more than 50 trees well

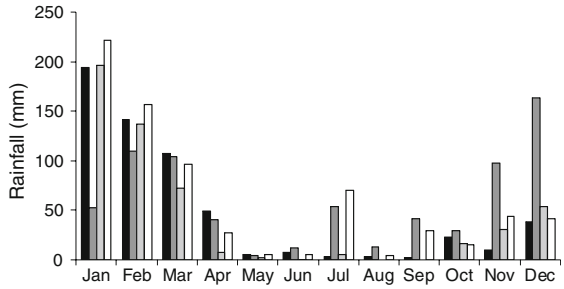

Fig. 1 Mean monthly rainfall (mm) at the four study sites in the Hluhluwe-iMfolozi Park from January to December 2004. Bars present data of different study sites; black: Nombali, dark grey: Maqanda, light grey: Mona, white: Tobothi. *Dichrostachys cinerea* seeds were sown mid of March 2004

spread over the HiP. Seeds were stored in a sealed box in a fridge for several days, scarified between sandpaper to break dormancy and imbibed in water for 12 h. A pre-germination test of *D. cinerea* seeds under controlled conditions revealed a germination rate of approximately 20% after 30 days.

The best time to conduct this study would have been to sow the seeds at the beginning of the wet season. However, flooding due to heavy rains forced us to sow the seeds later in the rainy season. Similarly, understanding when and under which conditions seedlings die may suggest factors influencing patterns of seedling establishment. A survival analysis makes it possible for us to monitor these patterns and also at what time of the year possible interacting effects take place.

Experiment 1: germination and survival of seedlings established from sown seeds

To examine the effects of herbivory and grass height on tree seedling germination and survival, two study sites were established in each mesic savanna in Hluhluwe (Nombali and Maqanda) and arid savanna in iMfolozi (Mona and Tobothi). Each study site had two large herbivore treatments: exclusion of large herbivores vs. unfenced control. Within the herbivore treatments four 1×1 m plots with tall grass and four 1×1 m plots with short grass were created by clipping the grass in half of the plots to approximately 8 cm grass height. A total of 64 plots were thus established. Plots inside and outside the herbivore exclosure were established with at least 10 m spacing to each other. The distance of the plots to the fences inside the exclosure was no less than 5 m. In mid-March, 25 imbibed seeds were sown in each plot (resulting in 1600 sown seeds in total) approximately 1 cm deep in the soil and watered. Seed germination, seedling survival and herbivory were monitored and vegetation height recorded in the plots on a monthly basis throughout the experiment (8 months). Seedlings were considered to be damaged by mammalian herbivores when their stems, leaves, or branches had been cut off and by invertebrates when leaves were partly eaten. If a seedling had lost one or more leaflets it was considered to be caused by partial wilting or disease. Wilted seedlings were also recorded.

Experiment 2: survival of transplanted seedlings

For this experiment one study site in mesic savanna (Nombali) and one study site in arid savanna (Mona) were used. Each study site had two herbivore treatments: exclusion of large herbivores vs. unfenced control. Within the herbivore treatments three 1×0.5 m plots with tall grass and three 1×0.5 m plots with short grass were created by clipping the vegetation to approximately 8 cm grass height. A total of 24 plots were thus established. Plots inside and outside the herbivore exclosure were established with at least 10 m spacing to each other. The distance of the plots to the fences inside the exclosure was no less than 5 m. Imbibed seeds were sown separately approximately 1 cm deep in plastic trays with soil from the park and stored in a nursery. Seeds were left to germinate and watered daily. After 8 weeks seedlings were approximately 2 cm in height. Nine seedlings were then transplanted in each 0.5×1 m plot into the field (resulting in 216 seedlings in total) and watered once a week during the first month. Because of the low number of seedlings transplanted our plot size requirements for this experiment was smaller than for experiment 1. Seedling survival, herbivory and vegetation height were monitored as described for experiment 1.

Data analysis

The effects of the treatments on time until germination and survival time of *Dichrostachys Cinerea* was analysed with Cox regression hazard model survival analyses. The model compared the number of seeds

that germinated with the number of seeds that did not germinate at a given time of the experiment (after Kleinbaum 1996). Furthermore, the number of seedlings that were alive at a given time was compared with the number of seedlings that had died. In those analyses germination time or survival time was the time factor, the status 'germinated' or 'alive' the event and herbivore exclusion (fenced vs. unfenced control), clipping treatment (clipped vs. unclipped control) and site the predictors. In the analysis of treatment effects on survival time, germination time was included as a covariate factor. The output of the model gives the coefficient estimates and associated estimated standard errors, chi-square statistics and *p*-values of Wald test. The higher the value of the Wald test the stronger the effect of the predictor(s) on the event. The survival analysis is designed to allow analyses before all events have been observed and to accommodate for the fact that not all seeds germinate at the same time. Because of these features, survival analysis was considered to be the most suitable method in this case, even if it was not possible to take the split-plot design of this experiment into account.

The effects of herbivore exclusion (fenced vs. unfenced control), clipping (clipped vs. unclipped control) and the interactions of site × clipping (herbivore exclusion) and site × herbivore exclusion on the proportion of seeds that germinated were analysed as a split-plot design. Clipping, clipping × exclosure, clipping × site, and clipping × exclosure × site were treated as effects within the herbivore exclosure treatment (at the sub-plot level), and herbivore exclusion, site and exclusion × site were treated as effects between the herbivore exclosure treatment (at the whole-plot level). Similar analyses were conducted for the proportion of seedlings that was still alive at the end of the wet season in April and at the end of the dry season in September, for both seedlings that established from sown seeds and transplanted seedlings. Too few seedlings remained at the end of the experiment (December) to be analysed statistically. The proportions of germinated seeds and seedlings were arcsine square-root transformed to normalise residuals. Seedling growth was tested using a factorial ANOVA with herbivore exclusion, clipping treatment and site as predictors and seedling height as dependent variable. Furthermore a Pearson's Chi-square test was used to analyse the overall differences of seedling damage in fenced/unfenced and clipped/unclipped plots.

Results

Experiment 1 – seed germination

The time of germination was not affected by the clipping treatment (Table 1). The effect of large herbivore exclusion on the time of seed germination varied among sites (significant site × herbivore exclusion interaction, Table 1). Germination started earlier in fenced plots compared to unfenced plots at all sites, but the germination rate levelled out in fenced plots at three sites (Maqanda, Mona and

Table 1 Effects of site, herbivore exclusion (fenced vs. unfenced control) and clipping treatment (clipped vs. unclipped control) on time of germination and survival time of *D. cinerea* over the course of the experiment (8 months), analysed with a Cox regression hazard model

Source of variation	df	Germination		Survival of seedlings established from seeds		Survival of transplanted seedlings	
		Wald	*P*	Wald	*P*	Wald	*P*
Site	1	6.953	*0.008*	0.05	0.823	3.674	0.055
Herbivore exclusion	1	3.631	0.057	10.74	*0.001*	1.351	0.245
Clipping	1	0.387	0.534	4.60	*0.032*	0.275	0.600
Site × Herbivore exclusion	1	4.295	*0.038*	14.94	*0.000*	3.522	0.610
Site × Clipping	1	2.658	0.103	0.52	0.472	3.621	0.570
Herbivore exclusion × Clipping	1	0.009	0.926	4.97	*0.026*	2.778	0.096
Site × Herbivore exclusion × Clipping	1	0.001	0.970	8.206	*0.004*	0.513	0.474
Germination time	1	–	–	36.91	*0.000*	–	–

P-values in italics are significant

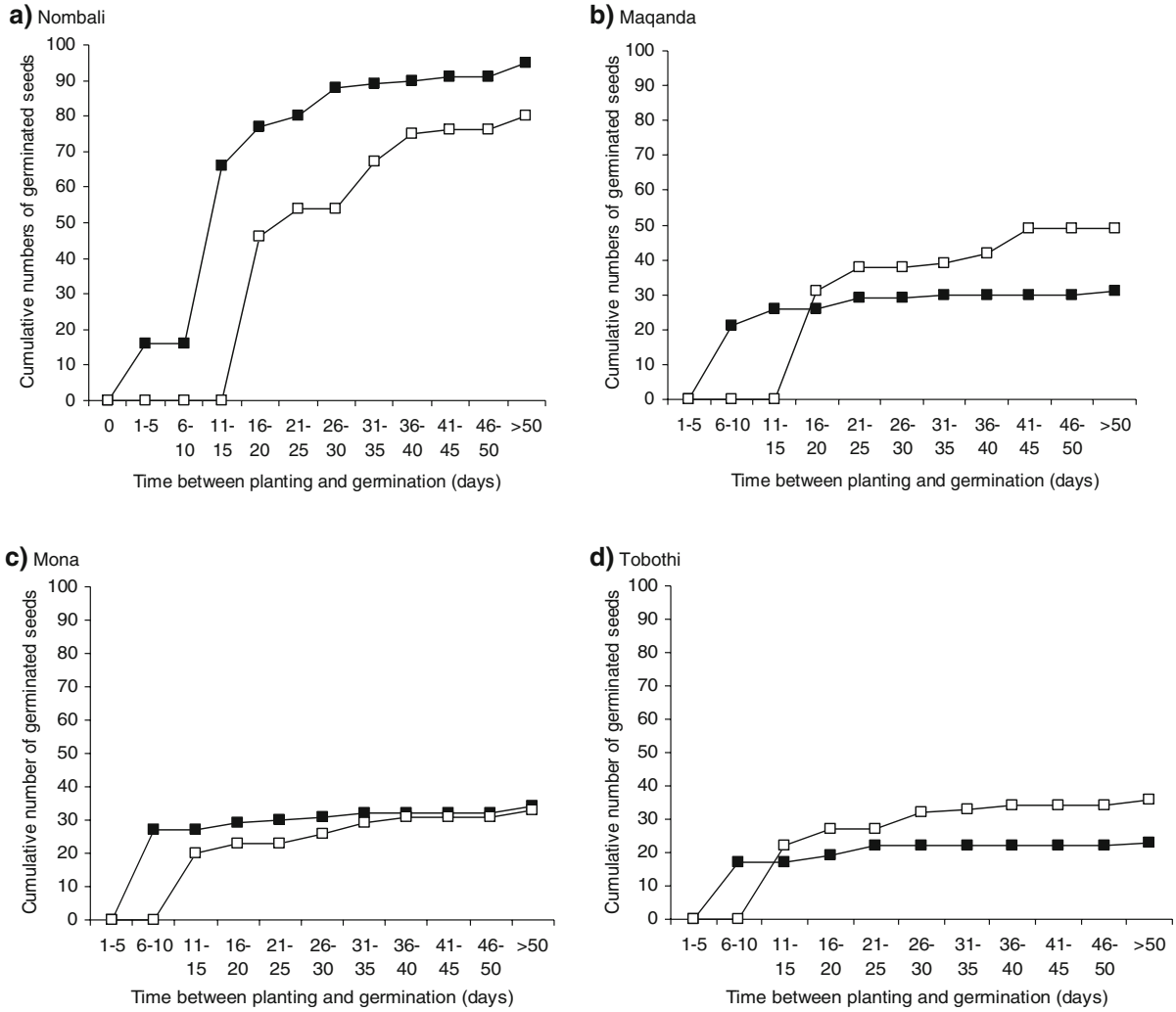

Fig. 2 Cumulative number of seeds that germinated in plots inside the large herbivore exclusion (solid squares) and unfenced control (open squares) within a given period after planting at the two mesic sites Nombali and Maqanda (**a** and **b**) and two arid sites Mona and Tobothi (**c** and **d**; $N = 380$)

Tobothi) after about a week. At Nombali the germination rate in fenced plots continued to be as high as in unfenced plots over the course of the experiment (Fig. 2a–d).

The proportion of seeds that germinated was positively affected by clipping and varied among sites (Table 2 and Fig. 3). At Nombali the proportion of germinated seeds was approximately 20% to 32% higher than at the three other sites, for unfenced and fenced plots, respectively (Fig. 3). For the first 15 days after seed planting, both the precipitation and the germination rate of seeds in fenced/unfenced plots were similar at all sites (Figs. 1, 2a–d). However, 16 to 25 days after seed planting, precipitation and seed germination rate was higher at the mesic sites than at the arid sites.

Experiment 1 – survival of seedlings established from sown seeds

Effect of germination time

Germination time affected time of survival of seedlings significantly (Table 1). Seedlings that established from seeds that germinated in the wet season had higher survival time than seedlings of germinated seeds from the dry season. Overall, the earlier the seeds germinated, the longer the seedlings survived.

Table 2 Experiment 1 (Seedlings established from sown seeds): Effects of site, herbivore exclusion (fenced vs. unfenced control) and clipping treatment (clipped vs. unclipped control) within the factor "herbivore exclusion", and of the between-subject factors "herbivore exclusion" and "site" on the total proportion of seeds that germinated and seedlings survived of *D. cinerea* at the end of the wet season (April) and at the end of the dry season (September), analysed with split-plot ANOVAs

Source of variation	df	Germination		Survival of seedlings established from seeds, April		Survival of seedlings established from seeds, September	
		F	*P*	*F*	*P*	*F*	*P*
Site	3	11.53	*0.000*	8.15	*0.001*	5.51	*0.005*
Herbivore exclusion	1	1.18	0.288	0.59	0.449	0.107	0.747
Clipping	1	5.32	*0.030*	9.11	*0.006*	19.30	*0.000*
Site × Clipping	3	0.185	0.906	2.44	0.089	4.34	*0.014*
Herbivore exclusion × Clipping	1	0.094	0.762	4.08	0.055	0.27	0.608
Site × Herbivore exclusion × Clipping	3	0.347	0.792	0.21	0.887	1.80	0.173
Herbivore exclusion × Site	3	0.69	0.565	1.67	0.201	3.01	*0.050*

P-values in italics are significant

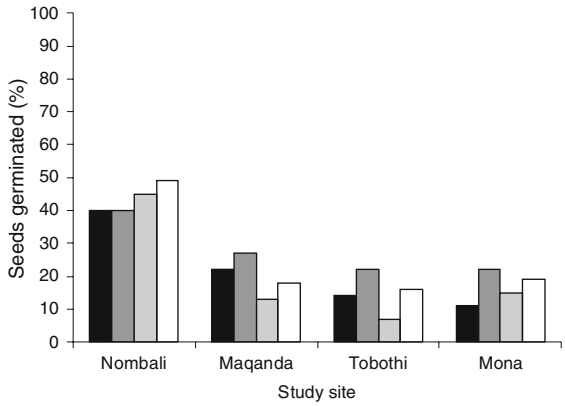

Fig. 3 Effects of the clipping treatment (clipped vs. unclipped) and exclusion of large herbivores (fence vs. unfenced) on the total percentage of *D. cinerea* seeds that germinated at two mesic sites (Nombali and Maqanda) and two arid sites (Tobothi and Mona). Bars present data of different combinations of treatments; black: unfenced, unclipped; dark grey: unfenced, clipped; light grey: fenced, unclipped; white: fenced, clipped

Interacting effects of clipping, herbivores and site

Seedling survival time was affected by large herbivore exclusion and clipping (Table 1). The combined effects of the grass clipping treatment and herbivore exclusion on the survival time of *D. cinerea* seedlings varied among sites (significant site × clipping treatment × herbivore exclusion interaction; Table 1). At the mesic site Nombali clipping had a positive effect on survival time where large herbivores were excluded, while at two other sites a positive clipping effect was found when herbivores were present (Fig. 4a–d).

The proportion of surviving seedlings was significantly higher in clipped than in unclipped grass and varied among sites, both at the end of the wet season and at the end of the dry season. There were also significant interactions between site and clipping treatment and between site and herbivore exclusion treatment at the end of the dry season (Table 2). In total only 21 seedlings that established from sown seeds were still alive at the end of the experiment in December, which was too few to analyse statistically. 13 of these seedlings were found at Nombali.

Cause of damage to seedlings

Overall, 32% of the seedlings were damaged. We observed significant differences in the damage types that seedlings experienced in the different treatments ($X^2_9 = 808.957$, $P < 0.000$, Fig. 5). For all treatments the most frequent damage to seedlings was leaflet loss because of wilting or disease. Most of the herbivory was caused by invertebrates but also mammals (most likely rodents) were found to be consumers of seedlings. Furthermore, both invertebrates and rodents damaged more seedlings in clipped than in unclipped grass, whereas the presence or absence of larger herbivores had no effect.

Experiment 2: survival of transplanted seedlings

Interacting effects of grass height, herbivores and site

There were no significant effects of treatments on survival time (Table 1; Fig. 6a, b). The effect of

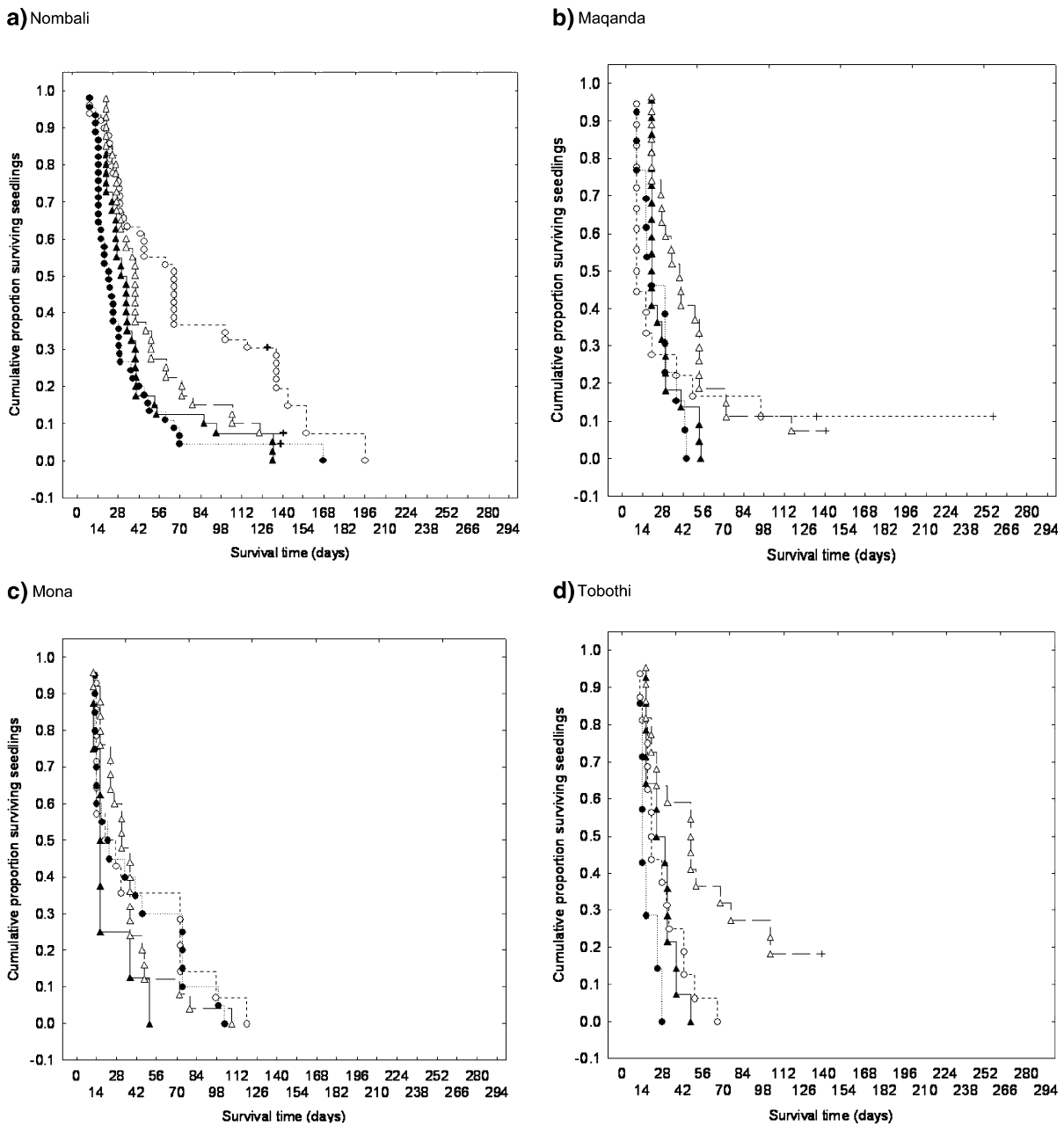

Fig. 4 Interacting effects of the clipping treatment (clipped vs. unclipped) and large herbivores (fence vs. unfenced) on the survival time of *D. cinerea* seedlings at the two mesic sites Nombali and Maqanda (**a** and **b**) and two arid sites Mona and Tobothi (**c** and **d**; Kaplan Meier). + = censored, other symbols = complete observations. Symbols present data of different combinations of treatments; *solid circles*: unclipped, fenced; *open circles*: clipped, fenced; *solid triangles*: unclipped, unfenced; *open triangles*: clipped, unfenced. The combined effects of the clipping treatment and large herbivore exclusion varied significantly among sites ($N = 380$, Wald = 8.206, $P = 0.004$)

clipping on the proportion of surviving seedlings in April varied among sites. In September, the proportion of surviving seedlings was not significantly affected by either treatments or interactions between them (Table 3). Only six transplanted seedlings were still alive at the end of the experiment; all of them

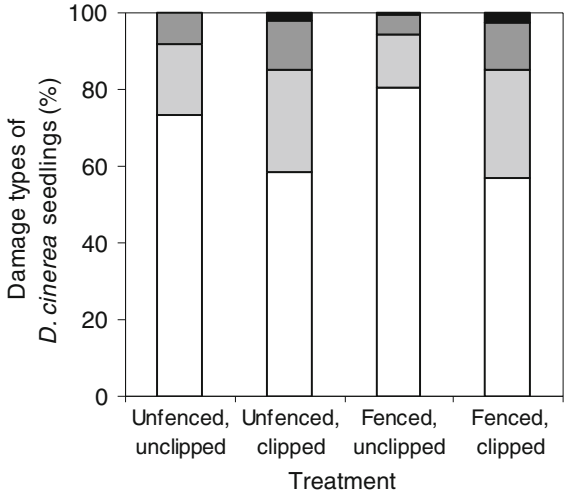

Fig. 5 Percentage of different damage types of *D. cinerea* seedlings for the different treatments at all sites for March to December 2004. *Black boxes*: rodent herbivory, *dark grey boxes*: invertebrate herbivory, *light grey boxes*: other damage, *white boxes*: no damage. Seedling damage was significantly different between treatments ($N = 890$, $X_9^2 = 808.957$, $P < 0.000$)

were recorded in clipped grass at the mesic site Nombali (Fig. 6a). This was too few to conduct further statistical analyses.

Seedling growth

Overall, seedling growth (as measured by height) was affected by both clipping treatment and site. Seedlings in clipped grass grew more than in unclipped grass plots ($F_{1,181} = 26.29$, $P < 0.001$) and seedling growth was higher at the mesic savanna site Nombali than at the arid savanna site Mona ($F_{1,181} = 10.06$, $P = 0.002$). We found no evidence that seedling growth was influenced by large herbivores.

Cause of damage to seedlings

Overall, 20% of the seedlings were damaged. Significant differences in the types of damage to seedlings in the different treatments were observed ($X_9^2 = 96.056$, $P < 0.000$, Fig. 7). Except for leaflet loss because of wilting or disease, most of the damage was caused by invertebrates. Rodent-type damage to seedlings was rarely observed. Furthermore, seedlings were more often damaged in unclipped than in clipped grass, and more seedlings were damaged in the absence of large herbivore than in their presence.

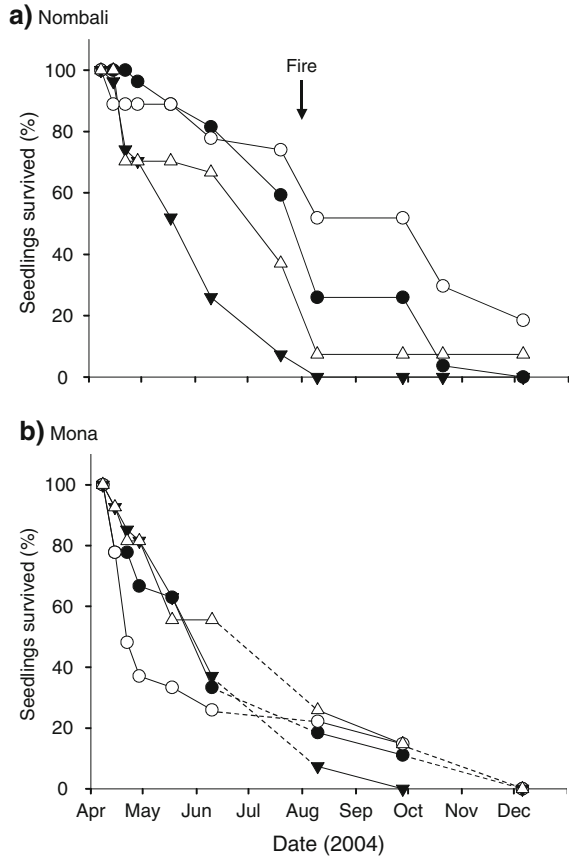

Fig. 6 Interacting effects of large herbivores (fence vs. unfenced) and clipping treatment (clipped vs. unclipped) on the survival of transplanted *D. cinerea* seedlings at the mesic site Nombali (**a**) and arid site Mona (**b**) for April to December 2004. Symbols present data of different combinations of treatments; *solid circles*: unclipped, fenced; *open circles*: clipped, fenced; *solid triangles*: unclipped, unfenced; *open triangles*: clipped, unfenced. The seedling survival at the two sites was not significantly influenced by the combined effects of the clipping treatment and large herbivore exclusion ($N = 3$ plots per treatment, Wald = 0.513, $P = 0.474$)

Discussion

Seed germination and seedling survival

It is often suggested that competitive inhibition by the grass layer may be a crucial filter for tree recruitment in savannas (Sankaran et al. 2005) but also herbivores have been considered important (Pellew 1983; Dublin 1991; McNaughton 1992; van Langevelde et al. 2003). In the present study, seed germination and seedling survival of *D. cinerea* was affected by the interplay of competition between trees and grasses for resources

Table 3 Experiment 2 (Transplanted seedlings): Effects of site, herbivore exclusion (fenced vs. unfenced control) and clipping treatment (clipped vs. unclipped control) within the factor "herbivore exclusion", and of the between-subject factors "herbivore exclusion" and "site" on total proportion of seedlings survived of *D. cinerea* at the end of the wet season (April) and at the end of the dry season (September), analysed with split-plot ANOVAs

Source of variation	df	Survival of transplanted seedlings, April		Survival of transplanted seedlings, September	
		F	*P*	*F*	*P*
Site	1	1.45	0.263	0.91	0.368
Herbivore exclusion	1	0.02	0.893	3.22	0.110
Clipping	1	1.14	0.318	3.24	0.110
Site × Clipping	1	52.12	*0.000*	0.16	0.704
Herbivore exclusion × Clipping	1	1.21	0.303	0.001	0.971
Site × Herbivore exclusion × Clipping	1	0.02	0.880	1.87	0.209
Herbivore exclusion × Site	1	1.26	0.295	0.000	0.984

P-values in italics are significant

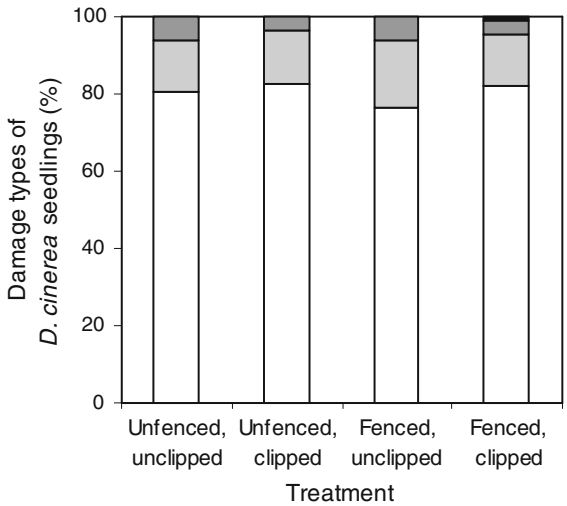

Fig. 7 Percentage of different damage types of *D. cinerea* seedlings for the different treatments at both sites for April to December 2004. *Black boxes*: rodent herbivory, *dark grey boxes*: invertebrate herbivory, *light grey boxes*: other damage, *white boxes*: no damage. Seedling damage was significantly different between treatments ($N = 366$, $X_9^2 = 96.056$, $P < 0.000$)

and habitat modifications caused by grazing large herbivores. For instance, by suppressing the growth of graminoids through intense grazing, herbivores may indirectly facilitate seed germination and seedling survival through improved light conditions. It has been shown that high light levels can improve seed germination and seedling survival (Denslow 1987; Brokaw 1985; Fischer et al. 1991; Belsky and Blumenthal 1997), which is demonstrated in our study. Furthermore, when the grass sward is damaged, e.g. by overgrazing, above- and below-ground biomass is reduced (Holland and Detling 1990) and more water becomes available for woody plants (Caldwell et al. 1987; Walker and Noy-Meir 1982; Bland 1985) that otherwise could have been utilised by the grasses (Walker and Noy-Meir 1982; Bland 1985). Water relations have been indicated to be particularly important during seed germination (Hoffmann 1996) and also for seedling survival. Therefore intense grazing by large herbivores may indirectly facilitate seed germination and seedling survival by suppressing the growth of competing grasses and thus accelerate tree recruitment through improved light and water availability.

On the other hand, grazing also can have negative effects on seedling survival. For instance, overgrazing often results in a significant decrease in vegetation cover and the lack of protective cover in turn may increase the seedlings' risk of being directly killed through trampling of large grazing herbivores. Additionally large grazers could graze them along with grasses and make them more visible to browsers. Furthermore, reduced shade levels in overgrazed areas may lead to higher desiccation which could promote a rise in seedling mortality when compared with a shady environment (Gerhardt 1996). In our study, seedling survival increased in clipped plots, but seedlings responded both negatively and positively to herbivore exclusion, indicating that the positive effects of herbivore presence on *D. cinerea* seed germination and seedling survival under some circumstances outweigh its negative effects but in other cases they did not.

In the first week of the study, seeds only germinated in the generally higher ungrazed grass inside the herbivore exclusion. The undisturbed grass sward might have kept the moisture and created a favourable microclimate for germination. After 2–3 weeks, coinciding with decreasing precipitation, germination rate in fenced plots slowed down in three of the four sites. The lighter rains at the beginning of dry season may not have reached the soil surface where the seeds were if the grass was dense, high and not disturbed by trampling. Because clipping had no significant effect on germination time, it appears that in this case trampling and thinning of the grass sward were more important factors than grass height. At Nombali, the germination rate was not affected by herbivore exclusion. This might be partly explained by the sometimes higher precipitation at this site. The total proportion of seeds that germinated was significantly affected by clipping but not by herbivore exclusion. The positive effect of early germination on survival time suggests that the total proportion of germinated seeds may be less important than a high germination rate at the beginning of the rainy season.

Seedling survival time of *D. cinerea* was affected by the interplay of competition between trees and grasses for resources and habitat modifications caused by grazing large herbivores. Overall, survival time was longer in clipped plots where large herbivores had access, as the combination of clipping and large herbivores resulted in short trampled grass that allowed rain and light to reach down to the soil surface. However, at Nombali survival time was longer in clipped plots in the absence of large herbivores. The positive effects of trampling seemed to be less important than the positive effects of clipping. These results are consistent with the expectations that less competition for light and water promotes seed germination and seedling survival. However, the high seedling mortality in this study may also partly be attributed to the late planting of the seeds.

Browsing mammals have been suggested to have a relatively low impact on tree seedling recruitment, while invertebrates may account for most of the herbivory (Miller 1994; Mucunguzi 1995; Meiners et al. 2000; Shaw et al. 2002). Roques et al. (2001) found that large browsers only had a minor impact on *D. cinerea* dynamics in Swaziland. In accordance with these studies we observed that invertebrates were responsible for most of the herbivory on *D. cinerea,* whereas large browsers were only of minor importance. Small mammals, most likely rodents, were found to be seedling predators. In African savannas the reported role of rodents in influencing tree recruitment ranges from potentially important (e.g. Miller 1994) to negligible (e.g. Barnes 2001). Shaw et al. (2002) found that rodents in East African savannas have only relatively little effects on *Acacia drepanolobium* seedling survival, whereas insects were considered to be important agents of seedling mortality.

Implications of the study

There is considerable debate on how rainfall (Fensham and Holman 1999; Fernandez-Gimenez and Allen-Diaz 1999; Fynn and O'Connor 2000) and grazing (Hulme et al. 1999; Bokdam and Gleichman 2000; Sternberg et al. 2000) should be taken into account in terms of management of shrub encroachment. The results of this study indicate that reductions in *D. cinerea* regeneration may occur when drought acts in concert with light grazing. Drought might inhibit germination of seeds and seedling survival. Light grazing may result in a closed grass sward that has the potential to reduce or prevent shrub encroachment (Roques et al. 2001) by out-competing seeds and seedlings for resources such as light. Furthermore, when the grass sward has sufficient above- and below-ground biomass the grasses would be able to utilise the water in the upper soil that otherwise would have been used by the woody species. Additionally, increased plant growth could lead to both increased fire frequencies (Roques et al. 2001) and intensities (Norton-Griffiths 1979) and fire would thus be another important tool to suppress bush encroachment.

In this study the grazing and browsing pressure during the early wet season, in addition to the absence of simulated grazing later on, affected the regeneration of *D. cinerea* negatively. The differences in effects among sites suggest that the mechanisms detected in this study may work differently in habitats with other conditions regarding grazing intensity, precipitation and invertebrate- and rodent herbivory. This is important to consider when planning land management to fight bush encroachment. Based on the results of our study it can be suggested that by modifying the vegetation structure large herbivores have an impact on the recruitment of *D. cinerea*. Managers can influence the grazing regime, but they

have little control over drought in order to prevent or reverse bush encroachment.

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